Studies on the Bionomics of *Tragidion armatum* LeConte (Coleoptera : Cerambycidae)

JOHN A. CHEMSAK AND JERRY A. POWELL University of California, Berkeley

Tragidion armatum LeConte, a large bright orange and black beetle, is widespread in desert areas from western Texas to southern California. Despite its showy appearance, the habits of this species have remained poorly known. Biological information is summarized by Linsley (1962) who states that the larvae make conspicuous burrows in dry stalks of Yucca and Agave. Of the six known species of Tragidion in the United States, only T. armatum uses Yucca and related plants as hosts. The remaining five are recorded as utilizing Quercus, Rhamnus, Prosopis, and Baccharis.

The broad geographical distribution of T. armatum indicates that a number of host species are used. In New Mexico, Townsend (1892) reared the beetle from Yucca angustifolia, while in California it has been recorded in association with Yucca whipplei (Coquillett, 1893; Fall, 1901; Hicks, 1929) and Y. brevifolia (Linsley, 1957, 1962). Linsley, et al. (1961) reported the rearing of T. armatum from an Agave in Arizona. Specimen records in the California Academy of Sciences and California Insect Survey indicate that Agave deserti is a host in southern California on the western margin of the Colorado Desert and that both Agave and "Dasylirion" are used in southern Arizona.

During extensive surveys in 1963 and 1964 of the three dominant California yuccas, Y. schidigera, Y. brevifolia, and Y. whipplei, Tragidion was found only in the latter two hosts in a restricted zone along the western edge of the Mojave Desert. Examination of Y. whipplei at numerous sites throughout its range in California indicated that this host species is used only along the eastern margins of its range, primarily where the distribution of Y. brevifolia or Agave deserti overlap that of Y. whipplei (Map 1). An additional Yucca, possibly elata, was verified as a host of T. armatum at a locality west of Wickenburg, Arizona, in July 1964.

Stalks of Y. whipplei and Y. brevifolia containing larvae of T. armatum were caged in the laboratory. Additional larvae successfully transformed into adults in dry pillboxes or when introduced into stalks of the same or a different host plant in the laboratory. Stalk sections of Agave or Y. whipplei were split longitudinally and a larva was placed in an artificial concavity gouged in the pith. The two halves were then

THE PAN-PACIFIC ENTOMOLOGIST 42: 36-47. January 1966

JANUARY 1966] CHEMSAK & POWELL—BIONOMICS OF TRACIDION 37

rejoined and taped together permitting the larvae to resume feeding. Observations on larval feeding were made and behavior of subsequently emerged adults was studied.

Adult Behavior

FLIGHT PERIOD.—Adults of T. armatum are reported as being active from April to August over the distributional range as a whole. However, California collection records and our data indicate that the species flies during April and early May in association with Y. brevifolia and in June and early July where Agave and Y. whipplei serve as hosts. It is probable that emergence is synchronized with host development in a manner enabling adults to be active when green flowering scapes are available. Adults have been reported on green stalks by Townsend (1892) and Coquillett (1893). Fall (1901) stated that beetles were active during blooming of the host.

MATING BEHAVIOR.—Observations on mating behavior were made on freshly emerged individuals in the laboratory. Successful matings were carried out on dry host plant material in cages and in cardboard containers as well.

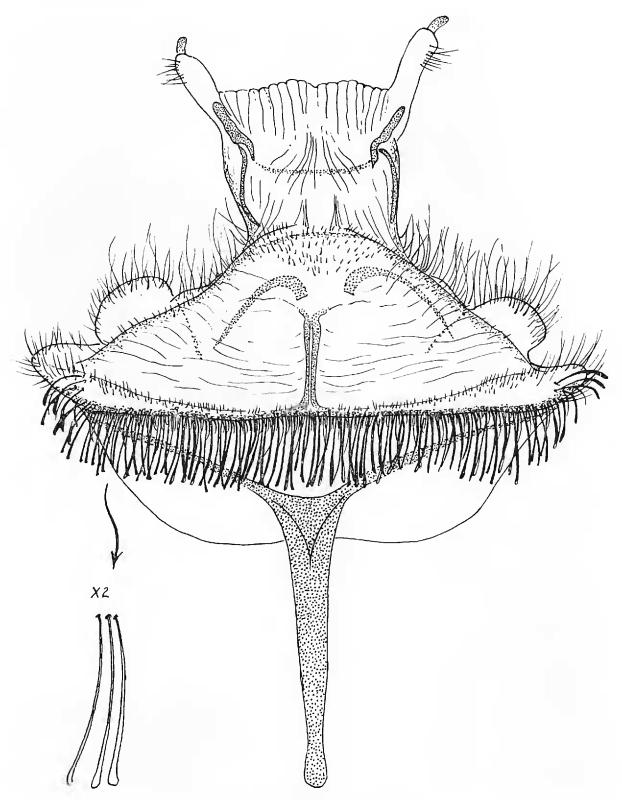
Copulation was usually attempted by the males at the first physical contact with the females. As soon as contact was made the male began to orient himself into the proper copulatory position. After mounting, the male clasped the female with his prothoracic and mesothoracic legs. The front pair usually grasped the pronotum or less often, the head, while the middle pair either hooked onto the middle coxae or went around the middle legs of the female. The antennae of the male were positioned out to the sides and slightly curved while those of the female were held back toward the body. Before successful coupling was accomplished the male maxillated the pronotum of the female with his palpi. This action apparently serves to pacify her since the process is repeated during copulation at signs of agitation or attempts to break away. A response on the part of the female was involved since successful joining was initiated when the female slightly distended the abdomen and spread the apical tergite and sternite. The male then placed the tip of the abdomen between the open sclerites of the female and inserted the phallus. A pulsating of the male abdomen was the only copulatory movement evident.

The duration of actual mating varied from 30 seconds to 3 minutes, but in most cases the pair maintained their positions for up to 10 minutes after disengagement of the genitalia. In many instances the same pair copulated more than once before the female dislodged the male. Also a female sometimes mated with more than one male before ovipositing.

OVIPOSITION.—The oviposition habits of the Cerambycidae have been categorized into two major types (Butovitsch, 1939; Linsley, 1959). These types may be basically summarized as (1) searching and oviposition exclusively with the ovipositor (most Cerambycidae) and (2) egg site selection and preparation with the aid of the ovipositor and mandibles (Lamiinae). Observations on oviposition behavior of *T. armatum* in the laboratory show that this function has features which are unlike those of other known cerambycids.

The ovipositor and accessory structures of the Purpuricenini are very distinctive, in fact may be considered as characteristic of this tribe, as well as the closely related tribes Pteroplatini, Trachyderini, Torneutini, some Platyarthrini, and the genera *Chrotoma* and *Chlorida*, presently assigned to the Hesperophanini. The apex of the eighth abdominal segment protrudes visibly between the apical abdominal sclerites. Its margin is provided with a fringe of setae. Those of the ventral margin are large, curved, and bristle-like, visible even on dried specimens (Fig. 1). The function of this fringe has been unknown. The ovipositor is quite short (Fig. 1) and appears to be incapable of being exerted beyond the apex of the fringe.

A dry stalk of Yucca whipplei was introduced during the day into a cage with a recently reared and mated female. She began searching for oviposition niches by arching the abdomen, slightly distending the fringed segment so the hairs were in contact with the substrate, and then proceeded to walk over the stalk. The purpose of this "sweeping" was not apparent until the egg was laid. When a suitable oviposition site was found, she stopped, slightly pulsated the abodmen, and deposited the egg. The ovipositor, though not visible during the process, probably serves to probe the plant surface for appropriate niches as it does in other cerambycids which lack the specialized bristle fringe of the eighth segment. The eggs when laid on the stalk surface were completely covered by an ovoid mount (2 mm by 1.5 mm and 1.5 mm high) of very fine granular dirt particles (Fig. 2). Subsequent examination of the genitalia and associated structures revealed an accumulation of fine, dark, dustlike debris in a pouch-like concavity between the bristle fringe and the ovipositor. Evidently the abdominal fringe when passed over the host plant surface (or in this case, possibly other surfaces within the cage) picks up small particles of dirt and debris. When the egg is deposited, a glutinous secretion is probably released which binds the

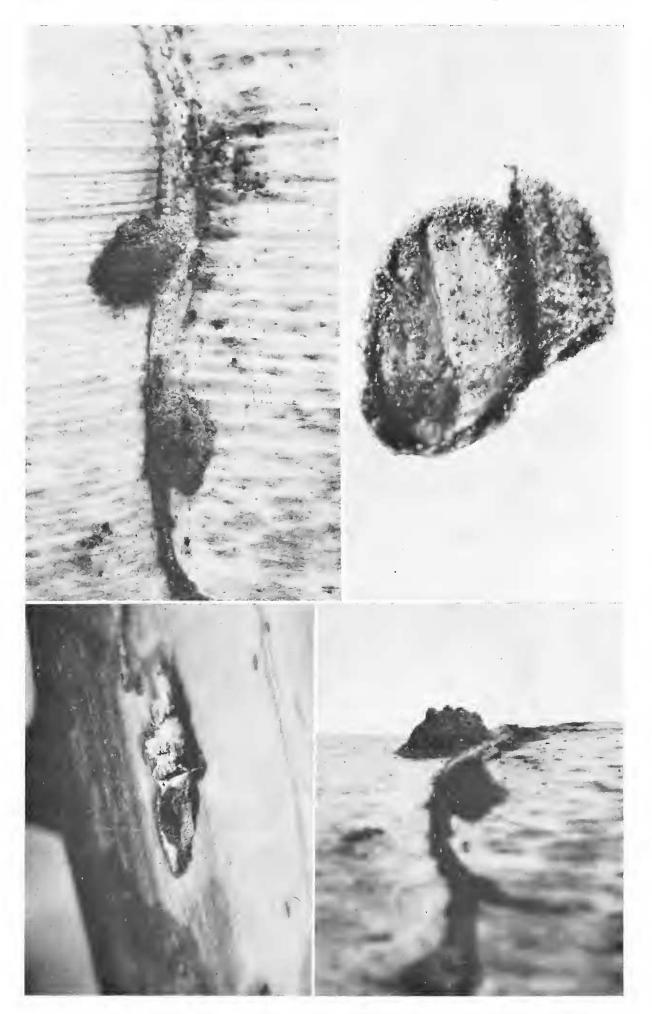


EXPLANATION OF FIGURE

Fig. 1. Distended ventral aspect of the eighth abdominal segment of female *Tragidion armatum* LeConte showing the setal fringe along the outside margin and portions of the genitalia.

particles together over the egg surface. This covering is shaped by the action of the internal eighth abdominal segment and ovipositor.

This behavior was confirmed by subsequent discovery of the eggs in the field at several sites, on three host species. These eggs were covered



41

by a much paler material resembling the sandy substrate characteristic of desert areas. Thus the oviposition behavior and associated structures of T. armatum are analagous to the tortricid moth Decodes fragarianus (Busck) (Powell, 1964). Females of Decodes and related genera were found to accumulate debris particles on the ovipositor pads by means of specialized setae. In most tortricids the setae of the ovipositor pads apparently function solely as sensory organs. As in the case of the moth, numerous genera related to Tragidion may be presumed to have similar habits on the basis of their similar structural modification.

During field observations in early July 1964, we found eggs at several localities. Previous knowledge of the appearance of the eggs in the laboratory made it relatively simple to find them in the field. Numerous eggs were found on the green, 1964 inflorescence stalks of Y. whipplei about five miles east of Gorman, Los Angeles County, California. The eggs were all deposited in depressions or scars on the stalk. Possibly some of these scars were made by adult gnawing as reported by Townsend (1892). The number of eggs ranged up to eight per stalk and most eggs were found below the inflorescence area. On 7 July these had not yet hatched.

At an area 21 miles east of Gorman, eggs were found on 1964 stalks of Y. brevifolia. All had been laid in cracked or split parts of the stalks and some were found on the side branches. These trees had six to eight eggs per stalk and early instar larvae were present in many of them. The presence of young larvae suggests that the eggs had been laid and hatched some time previously. Blooming of Y. brevifolia occurs in early April, at least a month ahead of Y. whipplei in this area. The flight period of adult beetles appears to vary correspondingly.

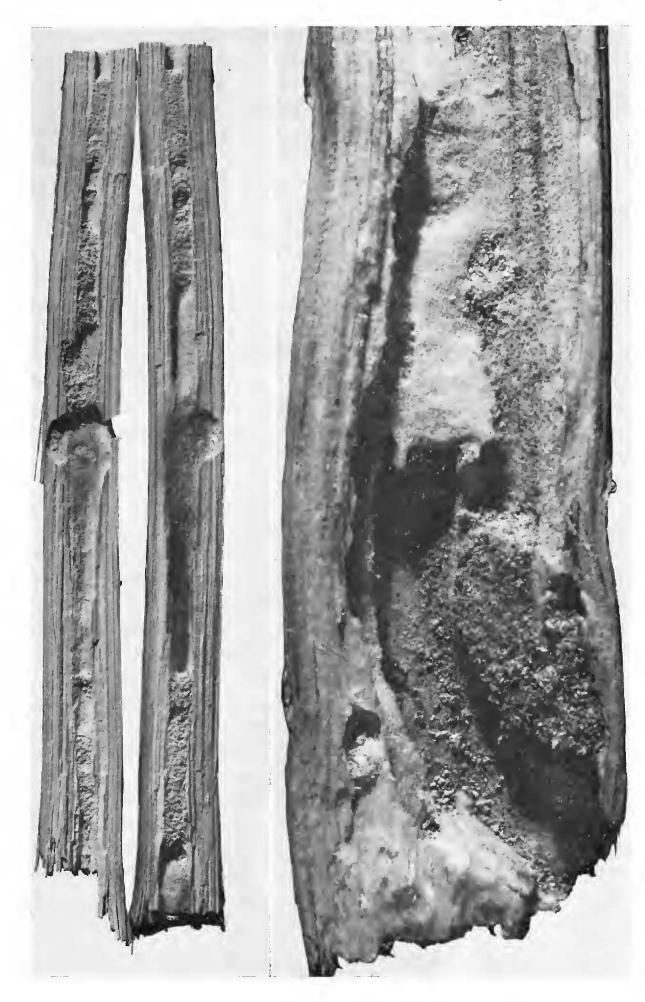
Observations were also made 6 miles west of Wickenburg, Arizona, on another *Yucca*, probably *elata*. Here also eggs were numerous on drying stalks in pits and scars. A number of the stalks had eggs deposited near the top of the inflorescence area.

The young larvae hatch out through the bottom of the egg and proceed to mine their way directly into the stalk. At this time the appearance of the eggs is unchanged with no evidence of hatching apparent externally. Those collected on 7 July were placed in salve tins still at-

←

EXPLANATION OF FIGURES

Fig. 2. Upper left: Dorsal view of eggs of *Tragidion armatum* LeConte laid along scar on *Yucca whipplei* stalk. Upper right: Underside view of *T. armatum* egg. Lower left: *T. armatum* egg laid in scar of a green *Y. whipplei* stalk. Lower right: Side view of *T. armatum* egg on *Y. whipplei* stalk.



tached to small strips of the stalk. The emergence of larvae 2 days later was possibly accelerated by desiccation of the plant material.

Flight records for adults suggest that a reasonable estimate of the duration of the egg stage would be 2–3 weeks in the field. According to Linsley (1961) the incubation period for eggs of most Cerambycidae ranges between 2 and 5 weeks.

LARVAL BEHAVIOR

The larva of *Tragidion armatum* has been described by Craighead (1923).

Upon hatching the larvae bore through the bottom of the egg, directly into the plant where they begin to feed in the pith. During feeding the larvae construct burrows which run with the longitudinal axis of the main scape, parallel with the monocotyledonous fibers. The lumen becomes tightly packed with frass along most of its length, but at intervals the gallery is empty (Fig. 3). In this study we found no cases of burrows opening to the exterior for frass exudation.

In Yucca whipplei half-grown larvae were discovered at various heights in the stalks, which usually range 2 to 3 meters in length. In the field larvae were generally more common in the lower, larger portions. In the laboratory larvae moved up and down the stalks alternately. Evidently the orientation while feeding is subject to change depending on the presence of available, unused pith. Many stalks were found to contain several *Tragidion* larvae, burrows of *Scyphophorus yuccae* Horn (Curculionidae), or externally damaged portions, etc., all of which act as factors in governing subsequent gallery formation.

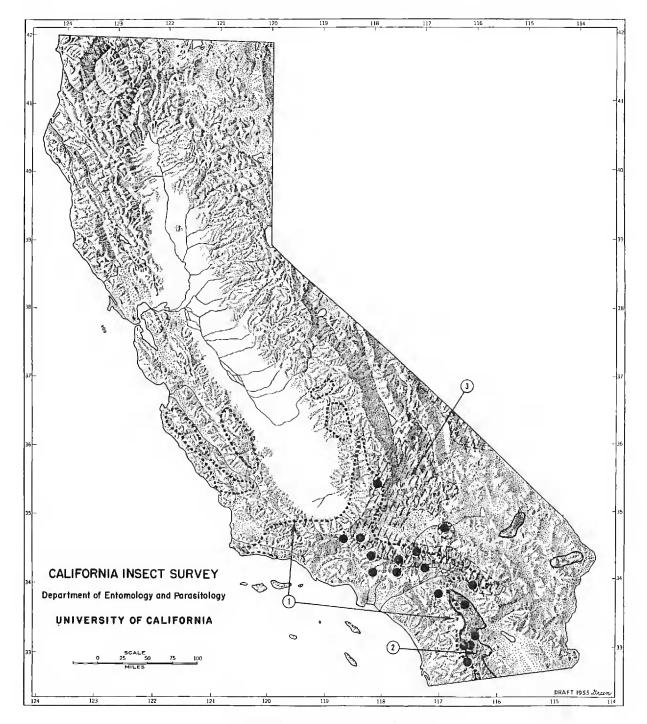
In Yucca brevifolia, the larger larvae were consistently found at the bases of dry inflorescence scapes, which are much shorter than in Y. whipplei, reaching to only about $\frac{1}{2}$ meter. The interior has a woody consistency, much denser than the soft pith of Y. whipplei, and the burrows constructed in Y. brevifolia are correspondingly shorter.

The pupation gallery is a broadened, hollow chamber which is constructed at the end of the feeding gallery (Fig. 3). The pupal chamber curves towards the external surface, leaving only a thin layer to be cut through by the emerging adult and there is no frass packing adjoining the exit. The size of the pupal chamber varies considerably according

EXPLANATION OF FIGURES

4

Fig. 3. Larval work of *Tragidion armatum* in *Yucca whipplei* stalk with pupal chamber and adult emergence hole at middle. Right: Pupal chamber of *T. armatum* in stalk of *Agave deserti*.



EXPLANATION OF MAP

Map 1. Distribution records of *Tragidion armatum* LeConte with the distribution limits of its host plants superimposed: 1, *Yucca whipplei*; 2, *Agave deserti*; 3, *Yucca brevifolia* (after Benson and Darrow, 1944).

to the size of the individual. Those feeding in Y. brevifolia apparently tend to be smaller. This size difference was pointed out by Linsley (1957) in characterizing the subspecies T. armatum brevipenne, an associate of Y. brevifolia.

According to Townsend (1892) and Linsley (1962) the life cycle of T. armatum requires one year. However, we have no direct evidence that larvae are able to complete development in one year. March and

JANUARY 1966] CHEMSAK & POWELL—BIONOMICS OF TRAGIDION

April collections of stalks produced the preceding year contained larvae of various sizes, but these failed to produce adults until the following year after storage at laboratory temperatures. A collection of Y. brevifolia scapes taken in March 1964 by R. W. Thorp included stalks of several seasons and was the only one of our caged lots from which the beetles emerged during the same year that the collection was made.

HOST PLANT RELATIONSHIPS

During the present investigation, we found no clear-cut preference for one species of Agavaceae by *Tragidion armatum* in California. As shown on Map 1, the occurrence of the beetle evidently is limited to the deserts and inland mountain areas marginal to the deserts. So far as known, the species does not follow *Yucca schidigera* and *Y. whipplei* to the coast in southern California nor into northern portions of the latter plant's distribution. *Yucca brevifolia* was found to be the most consistently used host (nearly every flowering stalk at some sites), but it was surveyed at only a few localities. However, consistent use of *Y. brevifolia*, and the restricted occurrence of the beetle on *Y. whipplei*, may be the result of factors associated with a desert environment and not to host preference.

The following is a list of localities where hosts were investigated for presence of *Tragidion armatum* during 1963 and 1964. Field surveys consisted of examination of several to many dry stalks during spring or fall months.

Agave deserti.—Riverside County: Pinyon Flat, 16 road miles southwest Palm Desert, April, negative; Decp Crcek, south of Palm Desert, April, larvae uncommon. San Diego County: 5 miles east Jacumba, March, negative. Arizona: Palm Cyn., Kofa Mountains, Yuma County, April, stalks scarce, one larva.

Nolina parryi.—Riverside County: Pinyon Flat, 16 road miles southwest Palm Desert, April, negative.

Yucca schidigera.—Riverside County: Pinyon Flat, 16 road miles southwest Palm Desert, April, negative. San Diego County: 4 miles west Jacumba, March, ncgative; 1 mile cast Boulevard, March, negative; Buckman Springs, March, negative; Telegraph Canyon, Chula Vista, March, negative.

Yucca brevifolia.---Los Angeles County: 21 miles east Gorman, March, July, larvae common; 22 miles east Gorman, March 1964, adults reared from old stalks. San Bernardino County: 1 mile southeast Desert Springs (=Pinon Hills), March, larvae common.

Yucca whipplei.—San Benito County: New Idria, April, negative. San Luis Obispo County: La Panza Camp, April, negative. Tulare County: Fairview, April, negative. Kern County: 4 miles west Miracle Springs, April, negative; 4 miles northeast Havilah, March 1963, April 1964, negative; 1 mile east Caliente, March, negative; Dove Springs Road, 1.5 miles east Kelso Vy., May, larvae uncommon. Los Angeles County: 5 miles east Gorman, March, larvae common; 1 mile south

Palmdale, March, larvae uncommon; 5 miles northwest Acton, March, negative; 5 miles north Solemint, March, negative; 4 miles northwest Topanga, April, negative. San Bernardino County: 1 mile southeast Desert Springs, March, larvae uncommon; Verdemont, March, negative. Riverside County: Citrus Exp. Sta., Riverside, March, negative; 10 miles southeast Valle Vista, April, negative; Santa Ana Mountains, west of Elsinore, March, negative. San Diego County: 5 miles northeast Fallbrook, March, negative; Cardiff-by-the-Sea, October, negative; 2 miles southeast El Cajon, October, negative; Buckman Springs, March, October, negative.

As discussed elsewhere (Powell and Mackie, 1965) areas of Yucca whipplei occupied by the subspecies Y. w. caespitosa are characterized by much more abundant bloom each year than is consistent in the typical race. Individual plants of the cespitose form, which occurs along the western edge of the Mojave Desert (Dove Springs, Gorman, Palmdale, Desert Springs, etc.) commonly send up one to several flowering stalks each year, with the remainder of the clump of basal rosettes persisting. The typical form, which ranges through cismontane southern California, is completely solitary, and each individual dies after flowering once. Thus a more abundant and consistent supply of stalks is available to Tragidion in areas of Yucca whipplei caespitosa, and these are the populations which were found to support T. armatum during our study. The beetle was not found to be present in the solitary, cismontane form, although at least one collection of adults (Laguna Mountains near Mt. Laguna Post Office, San Diego County, June 1952, Powell) may represent such an association.

DISCUSSION

Tragidion armatum feeds in the larval stage in flowering scapes of various species of Agavaceae, including Agave, Dasylirion, and Yucca. The occurrence of T. armatum in California is apparently limited by factors other than availability of suitable host plants. As indicated in Map 1, Yucca whipplei is utilized only in areas marginal to the deserts, where the distributions of either Y. brevifolia or Agave deserti overlap or are nearly adjoining that of Y. whipplei.

From observations both in the field and in the laboratory, the period of development of T. armatum from egg to adult requires 2 years, at least for many individuals.

The modified eighth abdominal segment of T. armatum was found to be directly related to the oviposition habits. The setose fringe serves to accumulate sand particles from the substrate, which are then spread over the egg, forming a peaked mound. The discovery of the function of this fringe, as well as the oviposition behavior and the nature of the

JANUARY 1966] CHEMSAK & POWELL—BIONOMICS OF TRAGIDION

eggs, may be very significant. Not only may biological observations on the groups of Cerambycinae possessing this structure be aided, but concepts in the higher classification of the subfamily may be affected as well.

Acknowledgments

This work was carried out in part under National Science Foundation sponsored studies on North American Cerambycidae (Grant GB-2326). We also wish to acknowledge R. W. Thorp, University of California, Davis, for field collections and H. B. Leech, California Academy of Sciences, for the loan of specimens.

LITERATURE CITED

- BENSON, L., AND R. A. DARROW. 1944. A manual of southwestern desert trees and shrubs. Univ. Arizona Biol. Sci. Bull., 6: 1-411, figs.
- BUTOVITSCII, V. VON. 1939. Zur Kenntnis de Paarung, Eiablage und Ernährung der Cerambyciden. Entomol. Tidskr., 60: 206–258.
- COQUILLETT, D. W. 1893. On the pollination of Yucca whipplei in California. Insect Life, 5 (5): 311–314.
- CRAIGHEAD, F. C. 1923. North American cerambycid larvae. Canada Dept. Agr. Tech. Bull., (n.s.) 27: 1–238, figs.
- FALL, H. C. 1901. List of the coleoptera of southern California, with notes on habits and distribution and descriptions of new species. Occ. Papers Calif. Acad. Sci., 8: 1–282.
- HICKS, C. H. 1929. On the nesting habits of *Callanthidium illustre* (Cresson) (Hymenop.) Canadian Entomol., 61: 1-8.
- LINSLEY, E. G. 1957. New subspecies of Cerambycidae mostly from Southwestern United States. Coleop. Bull., 11: 33–36.
 - 1959. Ecology of Cerambycidae. Ann. Rev. Entomol., 4: 99-138.
 - 1961. The Cerambycidae of North America. Part I. Introduction. Univ. Calif. Publ. Entomol., 18: 1-97, figs.
 - 1962. The Cerambycidae of North America. Part III. Taxonomy and classification of the subfamily Cerambycinae, tribes Opsimini through Megaderini. Univ. Calif. Publ. Entomol., 20: 1–188, figs.
- LINSLEY, E. G., J. N. KNULL, AND M. STATHAM. 1961. A list of Cerambycidae from the Chiricahua Mountain Area, Cochise County, Arizona. Amer. Mus. Nov., 2050: 1–34, figs.
- POWELL, J. A. 1964. Biological and taxonomic studies on tortricine moths, with reference to the species in California (Lepidoptera : Tortricidac) Univ. Calif. Publ. Entomol., 32: 318 p.
- POWELL, J. A., AND R. A. MACKIE. 1965. Biological interrelationships of moths and *Yucca whipplei*. Univ. Calif. Publ. Entomol. (in press).
- TOWNSEND, C. H. T. 1892. Biologic notes on New Mexico insects. Insect Life, 5 (1): 37-40.